2003. The Journal of Arachnology 31:305–308

SHORT COMMUNICATION

EFFECTS OF MATERNAL BODY SIZE ON CLUTCH SIZE AND EGG WEIGHT IN A PHOLCID SPIDER (*HOLOCNEMUS PLUCHEI*)

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ABSTRACT. The pholcid spider *Holocnemus pluchei* (Scopoli 1763) competes for food with conspecifics, and spiders reared on high food levels are generally larger. In this study, we examined whether larger female body size (as estimated by tibia-patella length) translated into increased reproductive success in the form of increased clutch size, clutch weight, and average egg weight. Larger spiders had more eggs and thus heavier clutches, but there was no relationship between maternal size and average egg weight. We also looked for a tradeoff between average egg weight and egg number, and we found a weak relationship in which average egg weight was highest for intermediate-sized clutches. Larger female body size thus translates into increased reproductive success in terms of egg number and clutch weight, but not weight of individual eggs.

Keywords: Pholcidae, fecundity, egg size, clutch size, fitness

Number and size of eggs produced are important components of spider fitness. Clutch size in most arthropod species, including spiders (Jann & Ward 1999; reviews in Marshall & Gittleman 1994; Simpson 1995) increases with female body size. In some arthropod species (Fox & Czesak 2000), including *Agelena limbata* Thorell (Tanaka 1995), females can alter investment in individual eggs based on maternal body size and condition, whereas in other arthropod species egg size is invariant (reviewed in Fox & Czesak 2000). Life history theory predicts tradeoffs between clutch size and offspring size (Smith & Fretwell 1974), although these are frequently not apparent (Fox & Czesak 2000).

We examined the effect of maternal body size on clutch size and average egg weight in the pholcid spider *Holocnemus pluchei*. (Scopoli 1763). The behavior and life history of this species is well known. Spiders often share webs and fight vigorously over prey and larger spiders generally win (Blanchong et al. 1995; Jakob 1991, 1994; Jakob et al. 2000). Spiders reared on higher prey levels grow to a larger size than spiders reared on lower prey levels, except for those on extremely limited food regimes that may add an additional instar before maturation (Jakob & Dingle 1990). Females in the laboratory readily mate multiply, and second male sperm priority predominates (Kaster & Jakob 1997). Because *H. pluchei* shifts webs frequently and it is difficult to follow marked individuals for extended periods, lifespan and total number of clutches in the field is unknown. In the laboratory, spiders often live for over a year, and we have occasionally observed individuals to lay multiple clutches (Jakob pers. obs.).

We were interested in linking more directly the behaviors of group living and fighting with their fitness consequences by establishing whether an increase in maternal body size translates into more eggs or heavier clutches. We were also interested in whether there were relationships among body size, clutch size and mean egg size. In other species, egg and offspring size has numerous fitness consequences, with larger generally being better (reviewed in Tanaka 1995). In *H. pluchei,* variation in offspring size or condition may have an additional consequence, because whether spiderlings join group webs or build their own webs depends significantly on their condition, which is in turn influenced by their recent feeding success (Jakob unpubl. data). Any variation in the resources allocated to individual eggs that affects the condition of the spiderlings might predispose newly independent individuals toward or away from group living.

During August of 1998, 57 female *Holocnemus pluchei* with egg sacs were collected on the campus

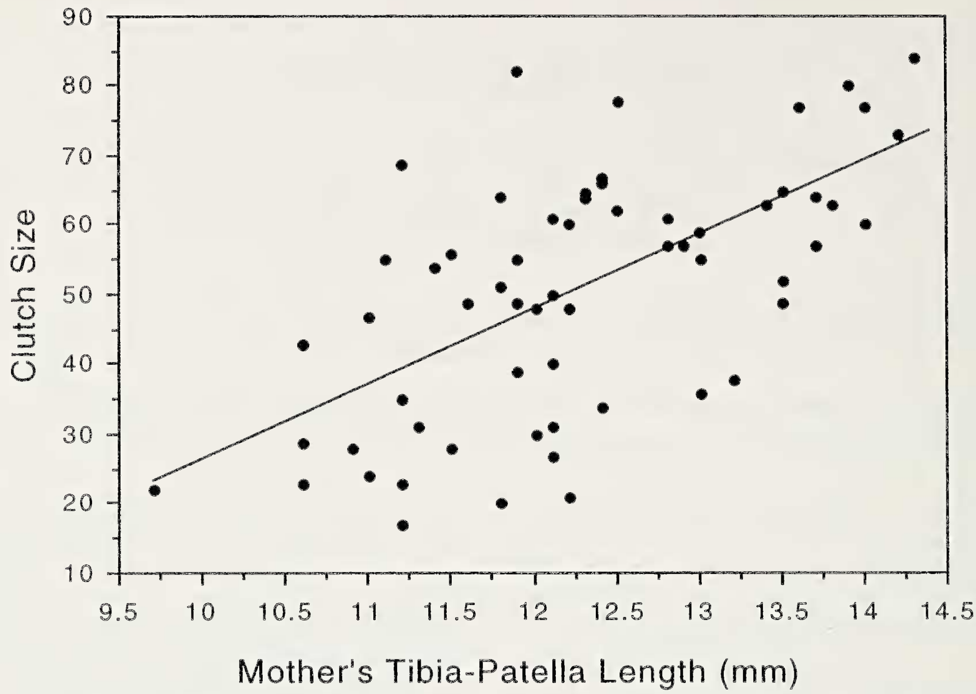

Figure 1.—Clutch size (number of eggs) regressed against mother's tibia-patella length.

of the University of California at Davis. Upon collection, 35 randomly chosen females were immediately anesthetized with carbon dioxide and preserved with their eggs in 95% ethanol in screw cap vials. The remaining 22 females were housed individually with their eggs as in Jakob (1991), and kept in growth chambers on a 15:9 L:D schedule with daytime temperatures of 32 °C and nighttime temperatures of 22 °C. All clutches hatched within four days of capture. Females normally do not feed while guarding and were not supplemented with food or water while in the chamber. When a clutch hatched, the female and her hatchlings were anesthetized with carbon dioxide and placed in screw cap vials (along with any unhatched eggs) with 95% ethanol for preservation. All samples were transported back to the University of Massachusetts at Amherst, where we measured female tibia-patella lengths of legs 1 and 2 with calipers, teased apart egg sacs and counted eggs, and counted hatchlings. After counting, we dried the females and their offspring in an oven at 128 °C for a minimum of 6 hours until they reached a constant weight. Samples were weighed on a microbalance within 24 hours of drying. Dried samples were kept in loosely capped vials in a sealed plastic container with silica gel (to prevent absorption of water) until being weighed. We weighed clutches rather than individual eggs or hatchlings because of the limits of scale accuracy. Some samples were inadvertently destroyed after counting and before weighing, so we weighed only 34 clutches of eggs and 22 clutches of hatchlings.

To estimate the size of the mother, we used female dry weight and tibia-patella lengths of legs 1 and 2. Tibia-patella length of leg 1 was highly correlated with leg 2 ($F_{1,60} = 892.76$, $R^2 = 0.968$, $P < 0.0001$), and with weight ($F_{1,60} = 80.391$, $R^2 = 0.573$, $P < 0.0001$), so for subsequent calculations we used only the tibia-patella length of leg 1.

We compared clutch size and clutch weight of offspring measured as eggs versus those measured as hatchlings and found no differences (clutch size: eggs 48 ± 2.8, hatchlings 53 ± 3.7, $F_{1,60} = 1.300$, $P > 0.2$; clutch weight: eggs 6.00 ± 0.002 mg, hatchlings 6.00 ± 0.002 mg, $F_{1,54} = 0.08$, $P > 0.7$). Nonetheless, because we were concerned that clutch weight might be affected by hatching, for all weight analyses we examined the two separate treatment groups as well as the pooled data. We found no qualitative differences in these analyses and present only the pooled data for brevity's sake.

We found that the mother's tibia-patella length of leg 1 significantly predicted both the number of eggs ($F_{1,60} = 36.574$, $R^2 = 0.379$, $P < 0.0001$, Fig. 1) and the total clutch weight ($F_{1,54} = 30.838$, $R^2 = 0.362$, $P < 0.0001$). The R^2 values indicate that a moderate amount of the variance is explained by maternal size, and is higher than or similar to that reported for other spiders (e.g., Buddle 2000; Tanaka 1995; Uetz and Hieber 1997).

These data provide a snapshot of a population in

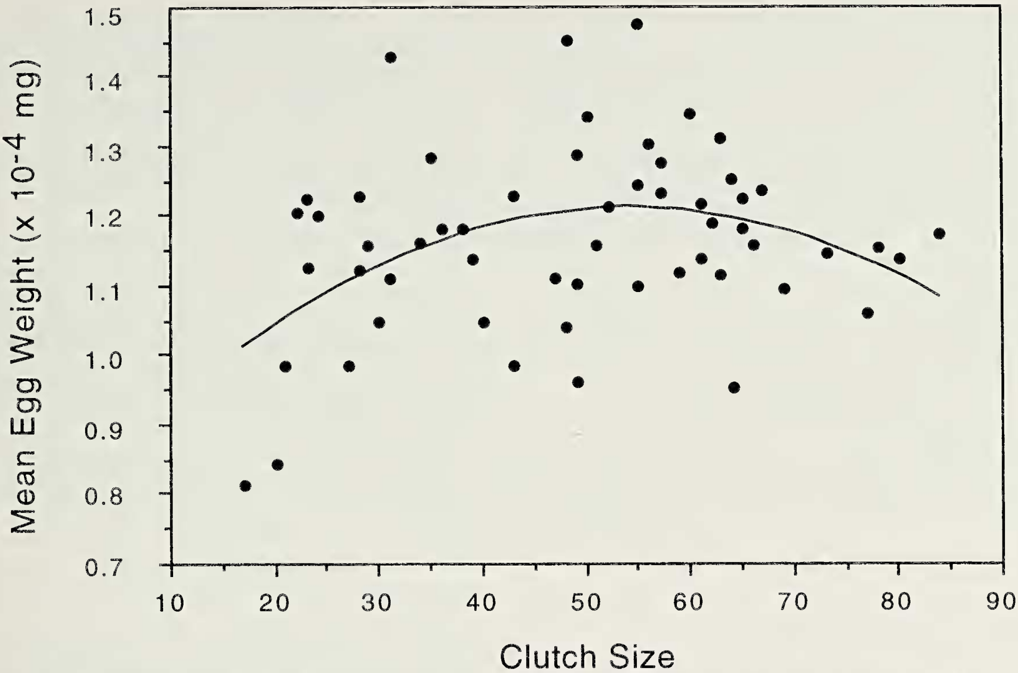

Figure 2.—Mean egg weight regressed against clutch size. There is no evidence of a classic egg weight/egg number tradeoff; average egg weight was highest for intermediate-sized clutches.

the field. Some of the variance probably results from the fact that our spiders were field caught. We could not control for many conditions likely to influence clutch size and weight, such as foraging history, temperature, female age and female parity (see Buddle 2000 for additional discussion). For example, spiders of all sizes are present year round, so it is likely that at the time of our collection in August there was a range of spider ages. In spite of this, the relationship between body size and clutch size is robust (Fig. 1), suggesting a fitness advantage of larger females under field conditions. However, if female size is negatively correlated with total number of clutches produced over a lifetime (e.g., if large females die younger) then this fitness benefit would be reduced or eliminated. This seems unlikely: in several cases where arthropod longevity and body size have been measured in the field, larger size correlates with longer lifespan, especially overwintering success (e.g., Ohgushi 1996).

We found no significant relationship between tibia-patella length and average egg weight ($F_{1,54}$ = 0.464, R^2 = 0.009, $P > 0.4$). In many arthropod populations, larger females lay larger eggs, but exceptions abound, and where there is a relationship it tends to be weak (reviewed in Fox & Czesak 2000). Given that our spiders were field caught and other important environmental variables were not controlled, we cannot definitively exclude a relationship between female body size and mean egg weight. However, we believe that a tradeoff is unlikely to be apparent under normal field conditions.

We looked for a tradeoff between egg size and number by regressing mean egg weight against clutch size. There was no significant linear relationship ($F_{1,55}$ = 2.905, $P > 0.09$). The data were best fit by a second order regression ($F_{3,55}$ = 3.455, R^2 = 0.166, $P < 0.01$, Fig. 2): intermediate clutch sizes had the highest mean egg weight. This is difficult to interpret, especially as different mechanisms may determine the shape of the curve at either end (for example, females in poor condition may only be able to lay few small eggs, whereas females laying large clutches may be constrained by abdominal volume). Only a small percent of the variance in mean egg weight is explained by clutch size. Other potential sources of variation include female age: in most arthropods, progeny size decreases with maternal age (Fox & Czesak 2000). Relationships between egg size and number can be difficult to detect because the total quantity of resources allocated to reproduction must be assumed to be constant, and this is unlikely to be true under field conditions (Fox & Czesak 2000). Further experiments will be needed to establish the robustness of this pattern and its underlying processes. In addition, the available microbalance did not allow us to measure individual eggs, and thus we cannot draw any conclusions about variation of egg size within female clutches.

In general, our findings are in line with the conclusions of Marshall & Gittleman (1994) that there is more flexibility in clutch size rather than egg size in spiders. Taken with previous studies of *H. pluchei* behavior and life history (Jakob & Dingle 1990), we conclude that there is a direct relationship between food intake, body size at maturity and reproductive success as measured by number of eggs and clutch weight. We have argued that spiders that are able to compete successfully for food have a selective advantage (Jakob 1991, 1994; Jakob et al. 2000), and this study provides additional support for this assumption for females.

ACKNOWLEDGMENTS

We thank B. Curtis for valuable assistance in the field. H. Dingle generously provided space in his laboratory. C. Yin kindly allowed us to use his balance, and D. Ferro loaned us his drying oven. We thank L. Baker, E. Wells, J. Houser, C. Hoefler, and A. Porter for comments on the manuscript, and M. Baker for insightful discussion. This study was supported by NSF IBN 95-07417 to EMJ.

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Manuscript received 12 September 2001, revised 11 December 2002.